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Permanence and periodicity of a delayed ratio-dependent predator–prey model with stage structure

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Abstract

A periodic ratio-dependent predator–prey model with time delays and stage structure for both prey and predator is investigated. It is assumed that immature individuals and mature individuals of each species are divided by a fixed age, and that immature predators do not have the ability to attack prey. Sufficient conditions are derived for the permanence and existence of positive periodic solutions of the model. Numerical simulations are presented to illustrate the feasibility of our main results.

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1. Introduction

Stage-structured models have received much attention in recent years (see, for example, [1,2,10,13,26–33]). This is not only because they are much simpler than the models

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governed by partial differential equations but also because they can exhibit phenomena similar to those of partial differential equations and many important physiological parameters can be incorporated [7]. The pioneering work of Aiello and Freedman [1] on a single species growth model with stage structure represents a mathematically more careful and biologically meaningful formulation approach. In [1], a model of single species population growth incorporating stage structure as a reasonable generalization of the classical logistic model was derived and investigated. This model assumes an average age to maturity which appears as a constant time delay reflecting a delayed birth of immatures and a reduced survival of immatures to their maturity. The model takes the form

$$\begin{aligned}\dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t - \tau), \\ \dot{x}_m(t) &= \alpha e^{-\gamma\tau} x_m(t - \tau) - \beta x_m^2(t), \quad t > \tau,\end{aligned}\tag{1.1}$$

where $x_i(t)$ represents the immature population density, $x_m(t)$ denotes the mature population density, $\alpha > 0$ represents the birth rate, $\gamma > 0$ is the immature death rate, $\beta > 0$ is the mature death and overcrowding rate, τ is the time to maturity. The term $\alpha e^{-\gamma\tau} x_m(t - \tau)$ represents the immature who were born at time $t - \tau$ and survive at time t (with the immature death rate γ), and therefore represents the transformation of immatures to matures.

The predator–prey systems are very important in the models of multi-species populations interactions and have been studied by many authors [15,19,20]. It is assumed in the classical predator–prey model that each individual predator admits the same ability to attack prey and each individual prey admits the same risk to be attacked by predator. This assumption is obviously unrealistic for many animals. In the natural world, there are many species whose individuals have a life history that take them through two stages, immature and mature, where immature predators are raised by their parents, and the rate they attack at prey and the reproductive rate can be ignored; on the other hand, it may be reasonable for a number of animals to assume that immature prey population concealed in the mountain cave and are raised by their parents; the rate of mature predators attacking at immature prey can be ignored. Recently, Wang and Chen [32] and Magnusson [29] proposed and investigated predator–prey models with stage structure to analyze the influence of a stage structure for predator on the dynamics of predator–prey models. But these models ignore the duration time of immature predators. In [33], a predator–prey model with stage structure for predator was derived and discussed by Wang et al. to show the effect of the duration time of immature predator on the global dynamics of predator–prey system. Sufficient conditions were derived in [33] for the permanence and global stability of a positive equilibrium of the proposed model. So far, most of the previous works on stage-structured ecological model deal with autonomous population systems. The analysis of these models has been centered around the coexistence of populations and the stability or attractivity of equilibria.

In population models, the standard Lotka–Volterra type models are very important and are often used by ecologists to describe interactions between predator and prey populations. Standard Lotka–Volterra type models, on which a large body of existing predator–prey theory is built by assuming that the per capita rate of predation depends on the prey numbers only. Recently, the traditional prey-dependent predator–prey models have been challenged by several biologists (see, for example, [4–6,16]) based on the fact that functional and numerical response over typical ecological time scales ought to depend on the densities

of both prey and predator, especially when predators have to search, share or compete for food. A more suitable general predator–prey model should be based on the “ratio-dependent” theory. This roughly states that the per capita predator growth rate should be a function of the ratio of prey to predator abundance. Moreover, as the number of predators often changes slowly (relative to prey number), there is often competition among the predators, and the per capita rate of predation should therefore depend on the numbers of both prey and predator, most probably and simply on their ratio. These hypotheses are strongly supported by numerous field and laboratory experiment and observations [3,4,6,18].

Based on the Michaelis–Menten or Holling type-II function, Arditi and Ginzburg [3] proposed a ratio-dependent function of the form

$$P\left(\frac{x}{y}\right) = \frac{c(x/y)}{m + (x/y)} = \frac{cx}{my + x}$$

and the following ratio-dependent predator–prey model:

$$\begin{aligned}\dot{x} &= x(a - bx) - cxy/(my + x), \\ \dot{y} &= y(-d + fx/(my + x)).\end{aligned}\quad (1.2)$$

Here $x(t)$ and $y(t)$ represent the densities of the prey and the predator at time t , respectively. a/b is the carrying capacity, $d > 0$ is the death rate of the predator, and a , c , m and f/c are positive constants that stand for the intrinsic growth rate of the prey, capturing rate, half saturation constant and conversion rate of the predator, respectively.

The ratio-dependent predator–prey models with or without time delays have been studied by many researchers recently and very rich dynamics have been observed (see, for example, [8,9,12,21–25,34–37] and references cited therein).

We note that any biological or environmental parameters are naturally subject to fluctuation in time. As Cushing [11] pointed out that it is necessary and important to consider models with periodic ecological parameters or perturbations which might be quite naturally exposed (for example, those due to seasonal effects of weather, food supply, mating habits, hunting or harvesting seasons, etc.). Thus, the assumption of periodicity of the parameters is a way of incorporating the periodicity of the environment.

Motivated by the recent work of Aiello and Freedman [1], the purpose of the present paper is to perform a global analysis of a ratio-dependent predator–prey model by incorporating stage structures for both prey and predator and periodicity of the environment into the model. To do so, we study the following delayed differential system:

$$\begin{cases} \dot{x}_1(t) = \alpha_1(t)x_2(t) - \gamma_1(t)x_1(t) - \alpha_1(t - \tau_1)e^{-\int_{t-\tau_1}^t \gamma_1(s)ds}x_2(t - \tau_1), \\ \dot{x}_2(t) = \alpha_1(t - \tau_1)e^{-\int_{t-\tau_1}^t \gamma_1(s)ds}x_2(t - \tau_1) - \beta_1(t)x_2^2(t) - \frac{a_1(t)x_2(t)y_2(t)}{my_2(t) + x_2(t)}, \\ \dot{y}_1(t) = \alpha_2(t)\frac{x_2(t)y_2(t)}{my_2(t) + x_2(t)} - \gamma_2(t)y_1(t) \\ \quad - \alpha_2(t - \tau_2)e^{-\int_{t-\tau_2}^t \gamma_2(s)ds}\frac{x_2(t - \tau_2)y_2(t - \tau_2)}{my_2(t - \tau_2) + x_2(t - \tau_2)}, \\ \dot{y}_2(t) = \alpha_2(t - \tau_2)e^{-\int_{t-\tau_2}^t \gamma_2(s)ds}\frac{x_2(t - \tau_2)y_2(t - \tau_2)}{my_2(t - \tau_2) + x_2(t - \tau_2)} - \beta_2(t)y_2(t), \end{cases}\quad (1.3)$$

where $x_1(t)$ and $x_2(t)$ denote the densities of immature and mature individual preys at time t , respectively; $y_1(t)$ and $y_2(t)$ represent the densities of immature and mature individual predators at time t , respectively. $\alpha_1(t)$, $\alpha_2(t)$, $\gamma_1(t)$, $\gamma_2(t)$, $\beta_1(t)$, $\beta_2(t)$, and $a_1(t)$

are continuously positive periodic functions with period ω . The model is derived under the following assumptions.

- (H1) The prey population: the birth rate into the immature population is proportional to the existing mature population with a proportionality $\alpha_1(t) > 0$; the death rate of the immature population is proportional to the existing immature population with a proportionality $\gamma_1(t) > 0$; the death rate of the mature population is of a logistic nature, i.e., it is proportional to square of the population with a proportionality $\beta_1(t)$. The term

$$\alpha_1(t - \tau_1)e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} x_2(t - \tau_1)$$

represents the number of immature preys that were born at time $t - \tau_1$ which still survive at time t and are transferred from the immature stage to the mature stage at time t . We refer to the article of Liu et al. [27]. The mature predators feed on the mature prey only.

- (H2) The predator population: the death rate of the immature population is proportional to the existing immature population with a proportionality $\gamma_2(t) > 0$; $a_1(t)$ is the capturing rate of mature predator, m is the half capturing saturation constant, $\alpha_2(t)/a_1(t)$ is the rate of conversion of nutrients into the reproduction of the mature predator, $\beta_2(t)$ is the death rate of mature predators. The term

$$\alpha_2(t - \tau_2)e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{x_2(t - \tau_2)y_2(t - \tau_2)}{m y_2(t - \tau_2) + x_2(t - \tau_2)}$$

represents the number of immature predators that were born at time $t - \tau_2$ which still survive at time t and are transferred from the immature stage to the mature stage at time t . It is assumed in (1.3) that immature individual predators do not feed on prey and do not have the ability to reproduce.

The initial conditions for system (1.3) take the form of

$$\begin{aligned} x_i(\theta) &= \phi_i(\theta) \geq 0, & y_i(\theta) &= \psi_i(\theta) > 0, \\ \phi_i(0) &> 0, & i &= 1, 2, \theta \in [-\tau, 0], \end{aligned} \quad (1.4)$$

where $\tau = \max\{\tau_1, \tau_2\}$, $(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \in C([-\tau, 0], R_{+0}^4)$, the Banach space of continuous functions mapping the interval $[-\tau, 0]$ into R_{+0}^4 , where we define

$$R_{+0}^4 = \{(x_1, x_2, x_3, x_4): x_i \geq 0, i = 1, 2, 3, 4\}$$

and the interior of R_{+0}^4 ,

$$R_+^4 = \{(x_1, x_2, x_3, x_4): x_i > 0, i = 1, 2, 3, 4\}.$$

For continuity of initial conditions, we require

$$x_1(0) = \int_{-\tau_1}^0 \alpha_1(s)e^{-\int_s^0 \gamma_1(u) du} \phi_2(s) ds,$$

$$y_1(0) = \int_{-\tau_2}^0 \alpha_2(s) e^{-\int_s^0 \gamma_2(u) du} \frac{\phi_2(s) \psi_2(s)}{m \psi_2(s) + \phi_2(s)} ds. \quad (1.5)$$

We adopt the following notations throughout this paper:

$$\bar{f} = \frac{1}{\omega} \int_0^\omega f(t) dt, \quad f^L = \min_{t \in [0, \omega]} |f(t)|, \quad f^M = \max_{t \in [0, \omega]} |f(t)|,$$

where f is a continuous ω -periodic function.

The organization of this paper is as follows. In the next section, sufficient conditions are established for the positivity of solutions and the persistence of system (1.3) with initial conditions (1.4) and (1.5). In Section 3, by using Gaines and Mawhin's continuation theorem of coincidence degree theory, we show the existence of positive ω -periodic solutions of system (1.3) with initial conditions (1.4)–(1.5). Numerical simulations are presented to illustrate the feasibility of our main results. In Section 4, a brief discussion is given to conclude this work.

2. Uniform persistence

In this section, we will perform analysis on the permanence and extinction of system (1.3) with initial conditions (1.4) and (1.5).

Definition. System (1.3) is said to be permanent if there exists a compact region $D \subset \text{Int } R_+^4$ such that every solution $z(t)$ of (1.3) with initial conditions (1.4) and (1.5) eventually enters and remains in the region D .

Lemma 2.1. *Solutions of system (1.3) with initial conditions (1.4) and (1.5) are positive for all $t \geq 0$.*

Proof. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be a solution of system (1.3) with initial conditions (1.4) and (1.5). Set $\tau^* = \min\{\tau_1, \tau_2\}$. Let us first consider $y_2(t)$ for $t \in [0, \tau^*]$. It follows from the fourth equation of system (1.3) that

$$\begin{aligned} \dot{y}_2(t) &= \alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{\phi_2(t - \tau_2) \psi_2(t - \tau_2)}{m \psi_2(t - \tau_2) + \phi_2(t - \tau_2)} - \beta_2(t) y_2(t) \\ &\geq -\beta_2(t) y_2(t) \end{aligned} \quad (2.1)$$

since $\phi_2(\theta) \geq 0$, $\psi_2(\theta) > 0$ for $\theta \in [-\tau^*, 0]$. Therefore, a standard comparison argument shows that

$$y_2(t) \geq y_2(0) e^{-\int_0^t \beta_2(s) ds},$$

i.e., $y_2(t) > 0$ for $t \in [0, \tau^*]$.

By the second equation of system (1.3), for $t \in [0, \tau^*]$, we derive

$$\begin{aligned}\dot{x}_2(t) &= \alpha_1(t - \tau_1)e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} \phi_2(t - \tau_1) - \beta_1(t)x_2^2(t) - \frac{a_1(t)x_2(t)y_2(t)}{my_2(t) + x_2(t)} \\ &\geq -\beta_1(t)x_2^2(t) - \frac{a_1(t)x_2(t)y_2(t)}{my_2(t) + x_2(t)}\end{aligned}\quad (2.2)$$

since $\phi_2(\theta) \geq 0$ for $\theta \in [-\tau^*, 0]$. Therefore, a standard comparison argument shows

$$\begin{aligned}x_2(t) &\geq x_2(0) \exp \left\{ \int_0^t \left[-\beta_1(s)x_2(s) - \frac{a_1(s)y_2(s)}{my_2(s) + x_2(s)} \right] ds \right\} > 0 \\ &\text{for } t \in [0, \tau^*].\end{aligned}\quad (2.3)$$

By (1.5) and the first and the third equations of system (1.3), one can rewrite $x_1(t)$ and $y_1(t)$ as follows:

$$\begin{aligned}x_1(t) &= \int_{t-\tau_1}^t \alpha_1(s)e^{-\int_s^t \gamma_1(u) du} x_2(s) ds, \\ y_1(t) &= \int_{t-\tau_2}^t \alpha_2(s)e^{-\int_s^t \gamma_2(u) du} \frac{x_2(s)y_2(s)}{my_2(s) + x_2(s)} ds.\end{aligned}\quad (2.4)$$

Hence the positivity of $x_2(t), y_2(t)$ on $[-\tau^*, \tau^*]$ implies that of $x_1(t)$ and $y_1(t)$ for $t \in [0, \tau^*]$.

In a similar way we treat the intervals $[\tau^*, 2\tau^*], \dots, [n\tau^*, (n+1)\tau^*]$, $n \in N$. Thus, $x_1(t) > 0, x_2(t) > 0, y_1(t) > 0$ and $y_2(t) > 0$ for all $t \geq 0$. This completes the proof. \square

Lemma 2.2 [30]. Consider the following equation:

$$\dot{x}(t) = ax(t - \tau) - bx(t) - cx^2(t),$$

where a, b, c and τ are positive constants, $x(t) > 0$ for $t \in [-\tau, 0]$. We have

- (i) if $a > b$, then $\lim_{t \rightarrow +\infty} x(t) = (a - b)/c$;
- (ii) if $a < b$, then $\lim_{t \rightarrow +\infty} x(t) = 0$.

Lemma 2.3. Positive solutions of system (1.3) with initial conditions (1.4) and (1.5) are ultimately bounded.

Proof. Suppose $z(t) = (x_1(t), x_2(t), y_1(t), y_2(t))$ is any positive solution of system (1.3) with initial conditions (1.4) and (1.5).

Define

$$\rho(t) = x_1(t) + x_2(t) + y_1(t) + y_2(t).$$

Calculating the derivative of $\rho(t)$ along positive solutions of (1.3), we obtain

$$\begin{aligned}
\dot{\rho}(t) &= \alpha_1(t)x_2(t) - \gamma_1(t)x_1(t) - \beta_1(t)x_2^2(t) - \frac{a_1(t)x_2(t)y_2(t)}{my_2(t) + x_2(t)} \\
&\quad + \alpha_2(t)\frac{x_2(t)y_2(t)}{my_2(t) + x_2(t)} - \gamma_2(t)y_1(t) - \beta_2(t)y_2(t) \\
&\leq -\gamma_1^L x_1(t) + (\alpha_1^M + \alpha_2^M/m)x_2(t) - \beta_1^L x_2^2(t) - \gamma_2^L y_1(t) - \beta_2^L y_2(t). \quad (2.5)
\end{aligned}$$

For a positive constant ε ($\varepsilon < \min\{\gamma_1^L, \gamma_2^L, \beta_2^L\}$), it follows from (2.5) that

$$\dot{\rho}(t) + \varepsilon\rho(t) \leq (\varepsilon + \alpha_1^M + \alpha_2^M/m)x_2(t) - \beta_1^L x_2^2(t).$$

Therefore, there exists a positive constant A such that

$$\dot{\rho}(t) + \varepsilon\rho(t) < A,$$

which yields

$$\rho(t) < \frac{A}{\varepsilon} + \left(\rho(0) - \frac{A}{\varepsilon}\right)e^{-\varepsilon t}.$$

Hence, positive solutions of system (1.3) with initial conditions (1.4) and (1.5) are ultimately bounded, i.e., there exist positive constants T_1 and M_i ($i = 1, 2, 3, 4$) such that $x_i(t) \leq M_i$, $y_i(t) \leq M_{i+2}$ for $t > T_1$. \square

Theorem 2.1. *System (1.3) with initial conditions (1.4)–(1.5) is permanent provided that*

$$(H3) \quad m\alpha_1^L e^{-\gamma_1^M \tau_1} > a_1^M, \quad \alpha_2^L e^{-\gamma_2^M \tau_2} > \beta_2^M.$$

Proof. Suppose $z(t) = (x_1(t), x_2(t), y_1(t), y_2(t))$ is any solution of system (1.3) with initial conditions (1.4) and (1.5).

It follows from the second equation of system (1.3) that for $t > \tau_1$,

$$\frac{dx_2(t)}{dt} \geq \alpha_1^L e^{-\gamma_1^M \tau_1} x_2(t - \tau_1) - \beta_1^M x_2^2(t) - \frac{a_1^M}{m} x_2(t).$$

We consider the following auxiliary equation:

$$\frac{du(t)}{dt} = \alpha_1^L e^{-\gamma_1^M \tau_1} u(t - \tau_1) - \frac{a_1^M}{m} u(t) - \beta_1^M u^2(t).$$

By Lemma 2.2 we derive

$$\lim_{t \rightarrow +\infty} u(t) = \frac{\alpha_1^L e^{-\gamma_1^M \tau_1} - a_1^M/m}{\beta_1^M} := m_2^*.$$

By comparison, there exist a $T_2 > \tau_1$ and a positive constant $m_2 < m_2^*$ such that $x_2(t) > m_2$ for $t \geq T_2$. As a consequence, from the fourth equation of system (1.3) we derive for $t > T_2 + \tau_2$ that

$$\dot{y}_2(t) > \alpha_2^L e^{-\gamma_2^M \tau_2} \frac{m_2 y_2(t - \tau_2)}{m y_2(t - \tau_2) + m_2} - \beta_2^M y_2(t). \quad (2.6)$$

Note that

$$\dot{y}_2(t) \geq -\beta_2^M y_2(t),$$

which implies

$$y_2(t - \tau_2) \leq y_2(t)e^{\beta_2^M \tau_2} \quad \text{for } t \geq \tau_2. \quad (2.7)$$

It follows from (2.6) and (2.7) that

$$\begin{aligned} \dot{y}_2(t) &> \alpha_2^L e^{-\gamma_2^M \tau_2} \frac{m_2 y_2(t - \tau_2)}{m e^{\beta_2^M \tau_2} y_2(t) + m_2} - \beta_2^M y_2(t) \\ &= \frac{m_2 \alpha_2^L e^{-\gamma_2^M \tau_2} y_2(t - \tau_2) - m_2 \beta_2^M y_2(t) - m \beta_2^M e^{\beta_2^M \tau_2} y_2^2(t)}{m e^{\beta_2^M \tau_2} y_2(t) + m_2}. \end{aligned} \quad (2.8)$$

Consider the following auxiliary equation:

$$\frac{du(t)}{dt} = \frac{m_2 \alpha_2^L e^{-\gamma_2^M \tau_2} u(t - \tau_2) - m_2 \beta_2^M u(t) - m \beta_2^M e^{\beta_2^M \tau_2} u^2(t)}{m e^{\beta_2^M \tau_2} u(t) + m_2}.$$

A similar argument in the proof of Lemma 3.1 in [30] shows that

$$\lim_{t \rightarrow +\infty} u(t) = \frac{m_2(\alpha_2^L e^{-\gamma_2^M \tau_2} - \beta_2^M)}{m \beta_2^M e^{\beta_2^M \tau_2}}.$$

By the comparison principle, we derive

$$\liminf_{t \rightarrow \infty} y_2(t) \geq \frac{m_2(\alpha_2^L e^{-\gamma_2^M \tau_2} - \beta_2^M)}{m \beta_2^M e^{\beta_2^M \tau_2}} := m_4^*.$$

Hence, there exist a $T_3 > T_2 + \tau_2$ and a positive constant $m_4 < m_4^*$ such that $y_2(t) > m_4$ for $t \geq T_3$.

It follows from (2.4) that for $t \geq T_3 + \tau$,

$$\begin{aligned} x_1(t) &= \int_{t-\tau_1}^t \alpha_1(s) e^{-\int_s^t \gamma_1(u) du} x_2(s) ds \geq \int_{t-\tau_1}^t \alpha_1^L m_2 e^{-\gamma_1^M(t-s)} ds \\ &= \frac{\alpha_1^L m_2}{\gamma_1^L} (1 - e^{-\gamma_1^L \tau_1}) := m_1 \end{aligned}$$

and

$$\begin{aligned} y_1(t) &= \int_{t-\tau_2}^t \alpha_2(s) e^{-\int_s^t \gamma_2(u) du} \frac{x_2(s) y_2(s)}{m y_2(s) + x_2(s)} ds \geq \int_{t-\tau_2}^t \alpha_2^L e^{-\gamma_2^M(t-s)} \frac{m_2 m_4}{m m_4 + m_2} ds \\ &= \frac{\alpha_2^L m_2 m_4}{\gamma_2^L (m m_4 + m_2)} (1 - e^{-\gamma_2^L \tau_2}) := m_3. \end{aligned}$$

We now let

$$D = \{(x_1, x_2, y_1, y_2) \mid m_i \leq x_i \leq M_i, m_{i+2} \leq y_i \leq M_{i+2}, i = 1, 2\}.$$

Then D is a bounded compact region in R_+^4 which has positive distance from coordinate hyper-planes. From what has been discussed above, we obtain that there exists a $T >$

$T_3 + \tau_2$ such that if $t \geq T$, every positive solution of system (1.3) with initial conditions (1.4) and (1.5) eventually enters and remains in the region D . The proof is complete. \square

In the following, by using a similar method in the proof of Theorem 2.1 in Wang et al. [33], we present a simple result for the extinction of the predator.

Theorem 2.2. *Adult predator population will go to extinction if $\alpha_2^M e^{-\gamma_2^L \tau_2} < \beta_2^L$.*

Proof. Let $(x_1(t), x_2(t), y_1(t), y_2(t))$ be a positive solution of system (1.3) with initial conditions (1.4) and (1.5). It follows from the fourth equation of system (1.3) that

$$\dot{y}_2(t) \leq \alpha_2^M e^{-\gamma_2^L \tau_2} y_2(t - \tau_2) - \beta_2^L y_2(t).$$

Consider the following auxiliary equation:

$$\dot{y}(t) = \alpha_2^M e^{-\gamma_2^L \tau_2} y(t - \tau_2) - \beta_2^L y(t). \quad (2.9)$$

Since $\alpha_2^M e^{-\gamma_2^L \tau_2} < \beta_2^L$, we can choose a positive constant $q > 1$ such that $q\alpha_2^M e^{-\gamma_2^L \tau_2} < \beta_2^L$. Take $p(s) = q^2 s$, $V(y) = y^2$. Calculating the derivative of $V(y)$ along solutions of Eq. (2.9) we obtain

$$\dot{V}(y(t)) = 2(\alpha_2^M e^{-\gamma_2^L \tau_2} y(t)y(t - \tau_2) - \beta_2^L y^2(t)). \quad (2.10)$$

If $p(V(y(t))) > V(y(t + \theta))$ for $-\tau_2 \leq \theta \leq 0$, we have $|qy(t)| > |y(t + \theta)|$. Therefore, it follows from (2.10) that

$$\dot{V}(y(t)) \leq 2y^2(t)(q\alpha_2^M e^{-\gamma_2^L \tau_2} - \beta_2^L)$$

if $p(V(y(t))) > V(y(t + \theta))$ for $-\tau_2 \leq \theta \leq 0$. Since $q\alpha_2^M e^{-\gamma_2^L \tau_2} < \beta_2^L$, by Theorem 4.2 in Chapter 5 of [17], we can derive $\lim_{t \rightarrow \infty} y(t) = 0$. A standard comparison argument shows that $\lim_{t \rightarrow \infty} y_2(t) = 0$. This completes the proof. \square

3. Existence of periodic solutions

In order to obtain the existence of positive periodic solutions of system (1.3), for convenience, we shall summarize in the following a few concepts and results from [14] that will be basic for this section.

Let X, Y be real Banach spaces, let $L : \text{Dom } L \subset X \rightarrow Y$ be a linear mapping, and $N : X \rightarrow Y$ be a continuous mapping. The mapping L is called a Fredholm mapping of index zero if $\dim \text{Ker } L = \text{codim Im } L < +\infty$ and $\text{Im } L$ is closed in Y . If L is a Fredholm mapping of index zero and there exist continuous projectors $P : X \rightarrow X$, and $Q : Y \rightarrow Y$ such that $\text{Im } P = \text{Ker } L$, $\text{Ker } Q = \text{Im } L = \text{Im}(I - Q)$, then the restriction L_P of L to $\text{Dom } L \cap \text{Ker } P : (I - P)X \rightarrow \text{Im } L$ is invertible. Denote the inverse of L_P by K_P . If Ω is an open bounded subset of X , the mapping N will be called L -compact on $\bar{\Omega}$ if $QN(\bar{\Omega})$ is bounded and $K_P(I - Q)N : \bar{\Omega} \rightarrow X$ is compact. Since $\text{Im } Q$ is isomorphic to $\text{Ker } L$, there exists an isomorphism $J : \text{Im } Q \rightarrow \text{Ker } L$.

Lemma 3.1. Let $\Omega \subset X$ be an open bounded set. Let L be a Fredholm mapping of index zero and N be L -compact on $\bar{\Omega}$. Assume

- (a) for each $\lambda \in (0, 1)$, $x \in \partial\Omega \cap \text{Dom } L$, $Lx \neq \lambda Nx$;
- (b) for each $x \in \partial\Omega \cap \text{Ker } L$, $QNx \neq 0$;
- (c) $\deg\{JQN, \Omega \cap \text{Ker } L, 0\} \neq 0$.

Then $Lx = Nx$ has at least one solution in $\bar{\Omega} \cap \text{Dom } L$.

We are now in a position to state and prove our result on the existence of positive periodic solutions of system (1.3).

Theorem 3.1. Let (H3) hold. Then system (1.3) with initial conditions (1.4) and (1.5) has at least one strictly positive ω -periodic solution.

Proof. We first consider the following subsystem:

$$\begin{aligned}\dot{x}_2(t) &= \alpha_1(t - \tau_1)e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} x_2(t - \tau_1) - \beta_1(t)x_2^2(t) - \frac{a_1(t)x_2(t)y_2(t)}{my_2(t) + x_2(t)}, \\ \dot{y}_2(t) &= \alpha_2(t - \tau_2)e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{x_2(t - \tau_2)y_2(t - \tau_2)}{my_2(t - \tau_2) + x_2(t - \tau_2)} - \beta_2(t)y_2(t)\end{aligned}\quad (3.1)$$

with initial conditions

$$\begin{aligned}x_2(\theta) &= \phi_2(\theta), & y_2(\theta) &= \psi_2(\theta), \\ \phi_2(\theta) &\geq 0, & \psi_2(\theta) &> 0, & \phi_2(0) &> 0, & \theta \in [-\tau, 0].\end{aligned}\quad (3.2)$$

Let

$$u_1(t) = \ln[x_2(t)], \quad u_2(t) = \ln[y_2(t)]. \quad (3.3)$$

On substituting (3.3) into (3.1), we derive

$$\begin{aligned}\frac{du_1(t)}{dt} &= \alpha_1(t - \tau_1)e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} e^{u_1(t-\tau_1)-u_1(t)} - \beta_1(t)e^{u_1(t)} - \frac{a_1(t)e^{u_2(t)}}{me^{u_2(t)} + e^{u_1(t)}}, \\ \frac{du_2(t)}{dt} &= \alpha_2(t - \tau_2)e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{e^{u_1(t-\tau_2)+u_2(t-\tau_2)-u_2(t)}}{me^{u_2(t-\tau_2)} + e^{u_1(t-\tau_2)}} - \beta_2(t).\end{aligned}\quad (3.4)$$

It is easy to see that if system (3.4) has one ω -periodic solution $(u_1^*(t), u_2^*(t))^T$, then $z^*(t) = (x_2^*(t), y_2^*(t))^T = (\exp[u_1^*(t)], \exp[u_2^*(t)])^T$ is a positive ω -periodic solution of system (3.1). Therefore, in the following we first prove that system (3.4) has at least one ω -periodic solution.

To apply Lemma 3.1 to (3.4), we first define

$$X = Y = \{(u_1(t), u_2(t))^T \in C(R, R^2): u_i(t + \omega) = u_i(t), i = 1, 2\}$$

and

$$\|(u_1(t), u_2(t))^T\| = \max_{t \in [0, \omega]} |u_1(t)| + \max_{t \in [0, \omega]} |u_2(t)|,$$

where $|\cdot|$ denotes the Euclidean norm. Then it is easy to see that X and Y are Banach spaces with the norm $\|\cdot\|$. Let

$$L : \text{Dom } L \cap X \rightarrow X, \quad L(u_1(t), u_2(t))^T = \left(\frac{du_1(t)}{dt}, \frac{du_2(t)}{dt} \right)^T,$$

where $\text{Dom } L = \{(u_1(t), u_2(t))^T \in C^1(R, R^2)\}$ and $N : X \rightarrow X$,

$$N \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} e^{u_1(t-\tau_1)-u_1(t)} - \beta_1(t) e^{u_1(t)} - \frac{a_1(t) e^{u_2(t)}}{m e^{u_2(t)} + e^{u_1(t)}} \\ \alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{e^{u_1(t-\tau_2)+u_2(t-\tau_2)-u_2(t)}}{m e^{u_2(t-\tau_2)} + e^{u_1(t-\tau_2)}} - \beta_2(t) \end{bmatrix}.$$

Define

$$P \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = Q \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \frac{1}{\omega} \int_0^\omega u_1(t) dt \\ \frac{1}{\omega} \int_0^\omega u_2(t) dt \end{bmatrix}, \quad \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} \in X = Y.$$

It is not difficult to show that

$$\begin{aligned} \text{Ker } L &= \{x \mid x \in X, x = h, h \in R^2\}, \\ \text{Im } L &= \left\{ y \mid y \in Y, \int_0^\omega y(t) dt = 0 \right\} \quad \text{is closed in } Y, \end{aligned}$$

and

$$\dim \text{Ker } L = \text{codim Im } L = 2,$$

and P and Q are continuous projectors such that

$$\text{Im } P = \text{Ker } L, \quad \text{Ker } Q = \text{Im } L = \text{Im}(I - Q).$$

It follows that L is a Fredholm mapping of index zero. Furthermore, the inverse K_P of L_P exists and has the form $K_P : \text{Im } L \rightarrow \text{Dom } L \cap \text{Ker } P$,

$$K_P(y) = \int_0^t y(s) ds - \frac{1}{\omega} \int_0^\omega \int_0^t y(s) ds dt.$$

Then $QN : X \rightarrow Y$ and $K_P(I - Q)N : X \rightarrow X$ are given respectively by

$$\begin{aligned} QNx &= \begin{bmatrix} \frac{1}{\omega} \int_0^\omega \left[\alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} e^{u_1(t-\tau_1)-u_1(t)} - \beta_1(t) e^{u_1(t)} - \frac{a_1(t) e^{u_2(t)}}{m e^{u_2(t)} + e^{u_1(t)}} \right] dt \\ \frac{1}{\omega} \int_0^\omega \left[\alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{e^{u_1(t-\tau_2)+u_2(t-\tau_2)-u_2(t)}}{m e^{u_2(t-\tau_2)} + e^{u_1(t-\tau_2)}} - \beta_2(t) \right] dt \end{bmatrix}, \\ K_P(I - Q)Nx &= \int_0^t Nx(s) ds - \frac{1}{\omega} \int_0^\omega \int_0^t Nx(s) ds dt - \left(\frac{t}{\omega} - \frac{1}{2} \right) \int_0^\omega Nx(s) ds. \end{aligned}$$

Clearly, QN and $K_P(I - Q)N$ are continuous.

In order to apply Lemma 3.1, we need to search for an appropriate open, bounded subset Ω .

Corresponding to the operator equation $Lx = \lambda Nx$, $\lambda \in (0, 1)$, we have

$$\begin{aligned}\frac{du_1(t)}{dt} &= \lambda \left[\alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} e^{u_1(t-\tau_1)-u_1(t)} - \beta_1(t) e^{u_1(t)} \right. \\ &\quad \left. - \frac{a_1(t) e^{u_2(t)}}{m e^{u_2(t)} + e^{u_1(t)}} \right], \\ \frac{du_2(t)}{dt} &= \lambda \left[\alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{e^{u_1(t-\tau_2)+u_2(t-\tau_2)-u_2(t)}}{m e^{u_2(t-\tau_2)} + e^{u_1(t-\tau_2)}} - \beta_2(t) \right].\end{aligned}\quad (3.5)$$

Suppose that $(u_1(t), u_2(t))^T \in X$ is a solution of (3.5) for a certain $\lambda \in (0, 1)$. Integrating (3.5) over the interval $[0, \omega]$ we obtain

$$\begin{aligned}&\int_0^\omega \alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} e^{u_1(t-\tau_1)-u_1(t)} dt \\ &= \int_0^\omega \beta_1(t) e^{u_1(t)} dt + \int_0^\omega \frac{a_1(t) e^{u_2(t)}}{m e^{u_2(t)} + e^{u_1(t)}} dt,\end{aligned}\quad (3.6)$$

$$\int_0^\omega \alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{e^{u_1(t-\tau_2)+u_2(t-\tau_2)-u_2(t)}}{m e^{u_2(t-\tau_2)} + e^{u_1(t-\tau_2)}} dt = \int_0^\omega \beta_2(t) dt. \quad (3.7)$$

Since $(u_1(t), u_2(t))^T \in X$, there exist $\xi_i, \eta_i \in [0, \omega]$ such that

$$u_i(\xi_i) = \min_{t \in [0, \omega]} u_i(t), \quad u_i(\eta_i) = \max_{t \in [0, \omega]} u_i(t), \quad i = 1, 2. \quad (3.8)$$

Multiplying the first equation of (3.5) by $e^{u_1(t)}$ and integrating over $[0, \omega]$ gives

$$\begin{aligned}&\int_0^\omega \alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} e^{u_1(t-\tau_1)} dt \\ &= \int_0^\omega \beta_1(t) e^{2u_1(t)} dt + \int_0^\omega \frac{a_1(t) e^{u_1(t)+u_2(t)}}{m e^{u_2(t)} + e^{u_1(t)}} dt.\end{aligned}\quad (3.9)$$

It follows from (3.9) that

$$\int_0^\omega \beta_1(t) e^{2u_1(t)} dt < \int_0^\omega \alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} e^{u_1(t-\tau_1)} dt,$$

which yields

$$\beta_1^L \int_0^\omega e^{2u_1(t)} dt < \alpha_1^M e^{-\gamma_1^L \tau_1} \int_0^\omega e^{u_1(t-\tau_1)} dt = \alpha_1^M e^{-\gamma_1^L \tau_1} \int_0^\omega e^{u_1(t)} dt. \quad (3.10)$$

By using the inequalities

$$\left(\int_0^\omega e^{u_1(t)} dt \right)^2 \leq \omega \int_0^\omega e^{2u_1(t)} dt,$$

we derive from (3.10) that

$$\beta_1^L \left(\int_0^\omega e^{u_1(t)} dt \right)^2 < \alpha_1^M \omega e^{-\gamma_1^L \tau_1} \int_0^\omega e^{u_1(t)} dt,$$

which implies

$$\int_0^\omega e^{u_1(t)} dt \leq \frac{\alpha_1^M \omega e^{-\gamma_1^L \tau_1}}{\beta_1^L}, \quad u_1(\xi_1) \leq \ln \frac{\alpha_1^M e^{-\gamma_1^L \tau_1}}{\beta_1^L}. \quad (3.11)$$

It follows from (3.5), (3.6) and (3.11) that

$$\begin{aligned} \int_0^\omega |u_1'(t)| dt &< \int_0^\omega \left[\alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} e^{u_1(t-\tau_1)-u_1(t)} \right. \\ &\quad \left. + \beta_1(t) e^{u_1(t)} + \frac{a_1(t) e^{u_2(t)}}{m e^{u_2(t)} + e^{u_1(t)}} \right] dt \\ &= 2 \int_0^\omega \left[\beta_1(t) e^{u_1(t)} + \frac{a_1(t) e^{u_2(t)}}{m e^{u_2(t)} + e^{u_1(t)}} \right] dt \leq 2\beta_1^M \int_0^\omega e^{u_1(t)} dt + \frac{2\bar{a}_1 \omega}{m} \\ &\leq \frac{2\alpha_1^M \beta_1^M \omega e^{-\gamma_1^L \tau_1}}{\beta_1^L} + \frac{2\bar{a}_1 \omega}{m} := c_1. \end{aligned} \quad (3.12)$$

We derive from (3.11) and (3.12) that

$$u_1(t) \leq u_1(\xi_1) + \int_0^\omega |u_1'(t)| dt \leq \ln \frac{\alpha_1^M e^{-\gamma_1^L \tau_1}}{\beta_1^L} + c_1. \quad (3.13)$$

Noting that

$$\int_0^\omega \alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} e^{u_1(t-\tau_1)} dt = \int_0^\omega \alpha_1(t) e^{-\int_t^{t+\tau_1} \gamma_1(s) ds} e^{u_1(t)} dt,$$

it follows from (3.9) that

$$\begin{aligned} \int_0^\omega \beta_1(t) e^{2u_1(t)} dt &= \int_0^\omega \alpha_1(t) e^{-\int_t^{t+\tau_1} \gamma_1(s) ds} e^{u_1(t)} dt - \int_0^\omega \frac{a_1(t) e^{u_1(t)+u_2(t)}}{m e^{u_2(t)} + e^{u_1(t)}} dt \\ &\geq \alpha_1^L e^{-\gamma_1^M \tau_1} \int_0^\omega e^{u_1(t)} dt - \frac{a_1^M}{m} \int_0^\omega e^{u_1(t)} dt, \end{aligned}$$

which yields

$$e^{u_1(\eta_1)} \geq \frac{\alpha_1^L e^{-\gamma_1^M \tau_1} - a_1^M/m}{\beta_1^M},$$

i.e.,

$$u_1(\eta_1) \geq \ln \frac{\alpha_1^L e^{-\gamma_1^M \tau_1} - a_1^M/m}{\beta_1^M}. \quad (3.14)$$

We derive from (3.12) and (3.14) that

$$u_1(t) \geq u_1(\eta_1) - \int_0^\omega |u_1'(t)| dt \geq \ln \frac{\alpha_1^L e^{-\gamma_1^M \tau_1} - a_1^M/m}{\beta_1^M} - c_1. \quad (3.15)$$

This, together with (3.13), leads to

$$\max_{t \in [0, \omega]} |u_1(t)| < \max \left\{ \left| \ln \frac{\alpha_1^M e^{-\gamma_1^L \tau_1}}{\beta_1^L} \right| + c_1, \left| \ln \frac{\alpha_1^L e^{-\gamma_1^M \tau_1} - a_1^M/m}{\beta_1^M} \right| + c_1 \right\} := R_1. \quad (3.16)$$

Multiplying the second equation of (3.5) by $e^{u_2(t)}$ and integrating over $[0, \omega]$ gives

$$\begin{aligned} \int_0^\omega \beta_2(t) e^{u_2(t)} dt &= \int_0^\omega \alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{e^{u_1(t-\tau_2)+u_2(t-\tau_2)}}{m e^{u_2(t-\tau_2)} + e^{u_1(t-\tau_2)}} dt \\ &\leq \frac{\alpha_2^M e^{-\gamma_2^L \tau_2}}{m} \int_0^\omega e^{u_1(t-\tau_2)} dt = \frac{\alpha_2^M e^{-\gamma_2^L \tau_2}}{m} \int_0^\omega e^{u_1(t)} dt, \end{aligned}$$

which, together with (3.11), implies

$$u_2(\xi_2) \leq \ln \frac{\alpha_1^M \alpha_2^M \omega e^{-(\gamma_1^L \tau_1 + \gamma_2^L \tau_2)}}{m \beta_1^L \beta_2^L} := \ln d_1. \quad (3.17)$$

It follows from (3.5) that

$$\begin{aligned} \int_0^\omega |u_2'(t)| dt &< \int_0^\omega \left[\alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{e^{u_1(t-\tau_2)+u_2(t-\tau_2)-u_2(t)}}{m e^{u_2(t-\tau_2)} + e^{u_1(t-\tau_2)}} + \beta_2(t) \right] dt \\ &= 2\bar{\beta}_2\omega. \end{aligned} \quad (3.18)$$

Thus, from (3.17) and (3.18) we can obtain

$$u_2(t) \leq u_2(\xi_2) + \int_0^\omega |u_2'(t)| dt \leq \ln d_1 + 2\bar{\beta}_2\omega. \quad (3.19)$$

Multiplying the second equation of (3.5) by $e^{u_2(t)}$ and integrating over $[0, \omega]$ again we derive

$$\int_0^\omega \beta_2(t) e^{u_2(t)} dt = \int_0^\omega \alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} \frac{e^{u_1(t-\tau_2)+u_2(t-\tau_2)}}{m e^{u_2(t-\tau_2)} + e^{u_1(t-\tau_2)}} dt$$

$$\begin{aligned}
&\geq \alpha_2^L e^{-\gamma_2^M \tau_2} \int_0^\omega \frac{e^{u_1(\xi_1) + u_2(t - \tau_2)}}{m e^{u_2(\eta_2)} + e^{u_1(\xi_1)}} dt \\
&= \frac{\alpha_2^L e^{-\gamma_2^M \tau_2} e^{u_1(\xi_1)}}{m e^{u_2(\eta_2)} + e^{u_1(\xi_1)}} \int_0^\omega e^{u_2(t - \tau_2)} dt \\
&= \frac{\alpha_2^L e^{-\gamma_2^M \tau_2} e^{u_1(\xi_1)}}{m e^{u_2(\eta_2)} + e^{u_1(\xi_1)}} \int_0^\omega e^{u_2(t)} dt,
\end{aligned}$$

which, together with (3.15), leads to

$$u_2(\eta_2) \geq \ln \frac{(\alpha_1^L e^{-\gamma_1^M \tau_1} - a_1^M/m)(\alpha_2^L e^{-\gamma_2^M \tau_2} - \beta_2^M)}{m \beta_1^M \beta_2^M e^{c_1}} := \ln d_2. \quad (3.20)$$

It follows from (3.18) and (3.20) that

$$u_2(t) \geq u_2(\eta_2) - \int_0^\omega |u_2'(t)| dt \geq \ln d_2 - 2\bar{\beta}_2 \omega. \quad (3.21)$$

This, together with (3.18), leads to

$$\max_{t \in [0, \omega]} |u_2(t)| < \max\{|\ln d_1| + 2\bar{\beta}_2 \omega, |\ln d_2| + 2\bar{\beta}_2 \omega\} := R_2. \quad (3.22)$$

Clearly, R_1 and R_2 in (3.16) and (3.22) are independent of λ . Denote $M = R_1 + R_2 + R_0$, where R_0 is taken sufficiently large such that the unique solution $(u^*, v^*)^T$ of the system of algebraic equations

$$\begin{aligned}
\frac{1}{\omega} \int_0^\omega \alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} dt - \bar{\beta}_1 e^u - \frac{\bar{a}_1 e^v}{m e^v + e^u} &= 0, \\
\frac{1}{\omega} \int_0^\omega \alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} dt \frac{e^u}{m e^v + e^u} - \bar{\beta}_2 &= 0
\end{aligned} \quad (3.23)$$

satisfies $\|(u^*, v^*)^T\| = |u^*| + |v^*| < M$.

We now take $\Omega = \{(u_1(t), u_2(t))^T \in X : \|(u_1, u_2)^T\| < M\}$. This satisfies the condition (a) in Lemma 3.1. When $(u_1(t), u_2(t))^T \in \partial\Omega \cap \text{Ker } L = \partial\Omega \cap R^2$, $(u_1, u_2)^T$ is a constant vector in R^2 with $|u_1| + |u_2| = M$. Thus, we have

$$QN \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \frac{1}{\omega} \int_0^\omega \alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} dt - \bar{\beta}_1 e^{u_1} - \frac{\bar{a}_1 e^{u_2}}{m e^{u_2} + e^{u_1}} \\ \frac{1}{\omega} \int_0^\omega \alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} dt \frac{e^{u_1}}{m e^{u_2} + e^{u_1}} - \bar{\beta}_2 \end{bmatrix} \neq \begin{bmatrix} 0 \\ 0 \end{bmatrix}.$$

This proves that condition (b) in Lemma 3.1 is satisfied.

Taking $J = I : \text{Im } Q \rightarrow \text{Ker } L$, $(u_1, u_2)^T \rightarrow (u_1, u_2)^T$, a direct calculation shows that

$$\begin{aligned}
& \deg(JQN(u_1, u_2)^T, \Omega \cap \text{Ker } L, (0, 0)^T) \\
&= \deg\left(\left(\frac{1}{\omega} \int_0^\omega \alpha_1(t - \tau_1) e^{-\int_{t-\tau_1}^t \gamma_1(s) ds} dt - \bar{\beta}_1 e^{u_1} - \frac{\bar{a}_1 e^{u_2}}{m e^{u_2} + e^{u_1}}, \right.\right. \\
&\quad \left.\left. \frac{1}{\omega} \int_0^\omega \alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} dt \frac{e^{u_1}}{m e^{u_2} + e^{u_1}} - \bar{\beta}_2\right)^T, \Omega \cap \text{Ker } L, (0, 0)^T\right) \\
&= \text{sgn}\left\{\frac{m \bar{\beta}_1 e^{2u_1^* + u_2^*}}{\omega (m e^{u_2^*} + e^{u_1^*})^2} \int_0^\omega \alpha_2(t - \tau_2) e^{-\int_{t-\tau_2}^t \gamma_2(s) ds} dt\right\} = 1,
\end{aligned}$$

where $(u_1^*, u_2^*)^T$ is the unique solution of (3.23).

Finally, it is easy to show that the set $\{K_P(I - Q)Nx \mid x \in \bar{\Omega}\}$ is equicontinuous and uniformly bounded. By using the Arzela–Ascoli theorem, we see that $K_P(I - Q)N: \bar{\Omega} \rightarrow X$ is compact. Consequently, N is L -compact.

By now we have proved that Ω satisfies all the requirements in Lemma 3.1. Hence, (3.4) has at least one ω -periodic solution. Accordingly, system (3.1) has at least one positive ω -periodic solution.

Let $(x_2^*(t), y_2^*(t))^T$ be a positive ω -periodic solution of system (3.1). Then it is easy to verify that

$$x_1^*(t) = \int_{t-\tau_1}^t \alpha_1(s) e^{-\int_s^t \gamma_1(u) du} x_2^*(s) ds$$

and

$$y_1^*(t) = \int_{t-\tau_2}^t \alpha_2(s) e^{-\int_s^t \gamma_2(u) du} \frac{x_2^*(s) y_2^*(s)}{m y_2^*(s) + x_2^*(s)} ds$$

are also ω -periodic. Thus, $(x_1^*(t), x_2^*(t), y_1^*(t), y_2^*(t))^T$ is a positive ω -periodic solution of system (1.3) with initial conditions (1.4)–(1.5). This completes the proof. \square

Finally, we give some examples to illustrate the feasibility of our main results in Theorems 2.1, 2.2 and 3.1.

Example 1. In system (1.3), let $\alpha_1(t) = 3 + \sin t$, $\gamma_1 = 0.3$, $\beta_1 = 2$, $a_1 = 1$, $m = 2$, $\alpha_2(t) = 2 + \sin t$, $\gamma_2 = 0.1$, $\beta_2 = 0.3$, $\tau_1 = 0.5$, $\tau_2 = 0.3$. It is easy to verify that the coefficients of system (1.3) satisfy (H3). By Theorem 2.1, system (1.3) is permanent; by Theorem 3.1 we see that system (1.3) has at least one strictly positive 2π -periodic solution. Taking

$$(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \equiv (k_1, 0.6, k_2, 0.6), \quad (3.24)$$

where

$$\begin{aligned}
k_1 &= 18(1 - e^{-0.15}) + 60[-1 + e^{-0.15}(0.3 \sin 0.5 + \cos 0.5)]/109, \\
k_2 &= 4(1 - e^{-0.03}) + 20[-1 + e^{-0.03}(0.1 \sin 0.3 + \cos 0.3)]/101,
\end{aligned} \quad (3.25)$$

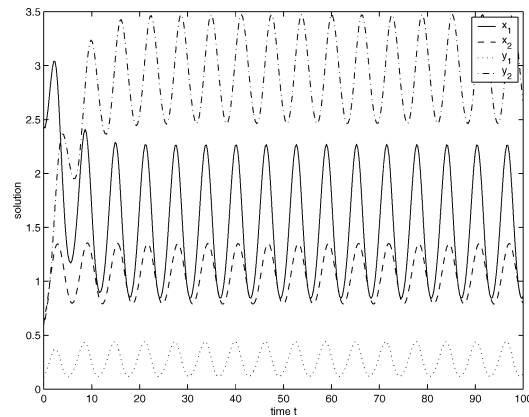


Fig. 1. The periodic solution found by numerical integration of system (1.3) with $\alpha_1(t) = 3 + \sin t$, $\gamma_1 = 0.3$, $\beta_1 = 2$, $a_1 = 1$, $m = 2$, $\alpha_2(t) = 2 + \sin t$, $\gamma_2 = 0.1$, $\beta_2 = 0.3$, $\tau_1 = 0.5$, $\tau_2 = 0.3$, $(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \equiv (k_1, 0.6, k_2, 0.6)$, where k_1 and k_2 are defined in (3.25).

numerical integration of system (1.3) with above coefficients can now be carried out using standard algorithms. We used the “dde23” package in MATLAB. As shown in Fig. 1, numerical simulation also suggests that system (1.3) with the coefficients above admits at least one strictly positive 2π -periodic solution.

Example 2. In system (1.3), we let $\alpha_1(t) = 3 + \sin t$, $\gamma_1 = 0.3$, $\beta_1 = 2$, $a_1 = 1$, $m = 2$, $\alpha_2(t) = 2 + \sin t$, $\gamma_2 = 0.1$, $\beta_2 = 3.1$, $\tau_1 = 0.8$, $\tau_2 = 0.6$. In this case, it is easy to verify that $\alpha_2^M = 3$, $\beta_2(t) \equiv 3.1$. By Theorem 2.2 we see that the adult predator will go to extinction. Taking

$$(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \equiv (k_3, 0.6, k_4, 0.6), \quad (3.26)$$

where

$$\begin{aligned} k_3 &= 18(1 - e^{-0.24}) + 60[-1 + e^{-0.24}(0.3 \sin 0.8 + \cos 0.8)]/109, \\ k_4 &= 4(1 - e^{-0.06}) + 20[-1 + e^{-0.06}(0.1 \sin 0.6 + \cos 0.6)]/101, \end{aligned} \quad (3.27)$$

numerical simulation also confirms that the adult predator population goes to extinction (see Fig. 2).

Example 3. In system (1.3), we let $\alpha_1(t) = 3 + \sin t$, $\gamma_1 = 0.3$, $\beta_1 = 2$, $a_1 = 3$, $m = 2$, $\alpha_2(t) = 2 + \sin t$, $\gamma_2 = 0.1$, $\beta_2 = 0.3$, $\tau_1 = 0.8$, $\tau_2 = 0.6$. It is easy to verify that (H3) does not hold for system (1.3). In this case, we cannot get any information by Theorems 2.1 and 3.1. However, if we take $(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \equiv (k_3, 0.6, k_4, 0.6)$, where k_1 and k_2 are defined in (3.27), numerical simulation suggests that system (1.3) with the above coefficients is still permanent and admits at least one strictly positive 2π -periodic solution (see Fig. 3).

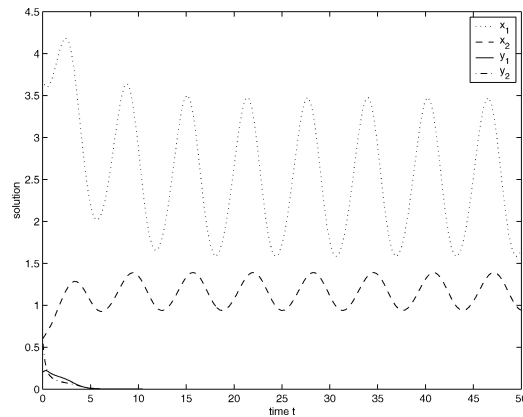


Fig. 2. The temporal solution found by numerical integration of system (1.3) with $\alpha_1(t) = 3 + \sin t$, $\gamma_1 = 0.3$, $\beta_1 = 2$, $a_1 = 1$, $m = 2$, $\alpha_2(t) = 2 + \sin t$, $\gamma_2 = 0.1$, $\beta_2 = 3.1$, $\tau_1 = 0.8$, $\tau_2 = 0.6$, $(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \equiv (k_3, 0.6, k_4, 0.6)$, where k_3 and k_4 are defined in (3.27).

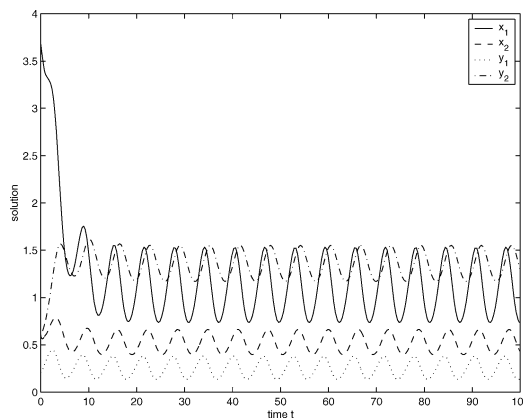


Fig. 3. The periodic solutions found by numerical integration of system (1.3) with $\alpha_1(t) = 3 + \sin t$, $\gamma_1 = 0.3$, $\beta_1 = 2$, $a_1 = 3$, $m = 2$, $\alpha_2(t) = 2 + \sin t$, $\gamma_2 = 0.1$, $\beta_2 = 0.3$, $\tau_1 = 0.8$, $\tau_2 = 0.6$, $(\phi_1(\theta), \phi_2(\theta), \psi_1(\theta), \psi_2(\theta)) \equiv (k_3, 0.6, k_4, 0.6)$, where k_3 and k_4 are defined in (3.27).

4. Discussion

In this paper, based on the work of Aiello and Freedman [1], we have incorporated the periodicity of the environment, stage structure for both prey and predator and time delays due to the maturities of prey and predator into a ratio-dependent predator–prey model. By some comparison technique, we have presented some results on the permanence and extinction of the system. By using Gaines and Mawhin's continuation theorem of coincidence degree theory, a set of easily verifiable sufficient conditions are derived for the existence of positive periodic solutions to the proposed model. By Theorem 2.1, we see that low mortality rates for juvenile prey and both adult and juvenile predators, high conversion rate of adult prey biomass into juvenile predators, short delays due to maturities for both

juvenile prey and predator, a low capturing rate of the adult predator, a high half saturation rate of the predator guarantee the permanence of the system. By Theorem 2.2 we see that the adult predator and juvenile predator will go to extinction if the conversion rate of adult prey biomass into juvenile predators is low, and the death rates of both adult and juvenile predator and the time delay due to maturity of the juvenile predators are high. By Theorem 3.1 we see that if system (1.3) is permanent, then it will admit at least one positive periodic solution.

We would like to mention here that Example 3 shows that our results in Theorems 2.1 and 3.1 have room for improvement; on the other hand, an interesting but challenging problem associated with the study of system (1.3) should be the uniqueness and global stability of positive periodic solutions. We leave these for future work.

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